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Catch-per-unit-effort and Biological Parameters from the Massachusetts Coastal Lobster (*Homarus americanus*) Resource: Description and Trends

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Catch-per-unit-effort and Biological Parameters from the Massachusetts Coastal Lobster (*Homarus americanus*) Resource: Description and Trends

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ABSTRACT

A comprehensive description of the Massachusetts coastal lobster (*Homarus americanus*) resource was obtained by sampling commercial catches coastwide at sea and at dealerships between 1981 and 1986. A commercial lobster sea-sampling program, wherein six coastal regions were sampled monthly, with an areal and temporal data weighting design, was the primary source of data.

An improved index of catch per trap haul/set-over-day was generated by modeling the relationship between catch and immersion time and standardizing effort. This 6-year time-series of mean annual catch rates tracked closely the landings trend for territorial waters.

During the study period there was a gradual increase in indices of exploitation and total annual mortality which corresponded to a gradual decline in mean carapace length of marketable lobster. The frequency of culls escalated from 10.0% in 1981 to 20.9% in 1986, while the percentage of lobster found dead in traps was consistently less than 1%. The sex ratio (%F:%M) was significantly different from 50:50 and approximated a 60:40 relationship during the study period.

Male and female weight-length relationships were significantly different. Females weighed more than males at smaller sizes and less than males at larger sizes. A north-south clinal trend was evident wherein lobster north of Cape Cod weighed less at length than those from regions south of Cape Cod.

Functional size-maturity relationships were developed for female lobster by staging cement gland development. Proportions mature at size represent more realistic values than those obtained by analyses of percent of females ovigerous.

Regional variation occurred in most of the parameters studied. Three lobster groups, differing in major population descriptors, are defined by our data.

Introduction

The American lobster (*Homarus americanus*) ranges over the continental shelf of the western North Atlantic ocean from Labrador to Cape Hatteras. Its biology and behavior have been extensively studied (Anthony and Caddy 1980, Cobb and Phillips 1980, Reinhart 1986). Specific information on its population dynamics was gathered by governmental researchers to formulate the American Lobster Fishery Management Plan (NEFMC 1983). However, with the exception of Maine and New York the detailed collection of long time-series of catch-effort and biological data was lacking among the lobster harvesting states.

Until recently, historical trend data on the lobster resource along the Massachusetts coast were limited to annual landings in number or pounds of lobster, total traps reported fished, and licensing statistics. A crude catch-per-unit-effort (CPUE) calculation (landings/traps reportedly fished) was available from these data. Additional data describing the fishery and resource were generated primarily through short-term research efforts involving sampling of lobster catches at dealerships or from commercial lobster traps at sea.

Since lobster supports the most economically important single species fishery in Massachusetts coastal waters, the regular assessment of the status of this resource is warranted. Accordingly, a long-term coastwide lobster monitoring program was devised and initiated by the Massachusetts Division of Marine Fisheries in May 1981. A structured, comprehensive sea sampling-survey design was chosen by which both CPUE and biological data could be collected temporally and areally with sufficient precision for stock assessment. The overall objective was to assess variation in population parameters due to environmental factors, fishing pressure, and regulatory changes.

This sampling program provided the core of the data discussed in this description of the Massachusetts coastal lobster resource. However, additional studies involved sampling and procedures which were beyond the scope of the sea-sampling effort and included special sampling at sea and at dealerships in association with laboratory analyses.

Methods

Study area

The study area is primarily defined by the Massachusetts territorial sea, except where lobstering activities of cooperating commercial lobstermen exceeded territorial boundaries (Fig. 1). Territorial waters total 5,322 km^2 (2,055 nmi^2), of which an estimated 60% is considered major lobster habitat. Six sampling regions—Cape Ann, Beverly-Salem, Boston Harbor, Cape Cod Bay, outer Cape Cod, and Buzzards Bay—were chosen for coverage of the major lobstering regions of the state. For convenience, these regions are depicted as generalized hatch-marked areas in Figure 1 wherein lobster gear sampled may be discontinuously distributed.

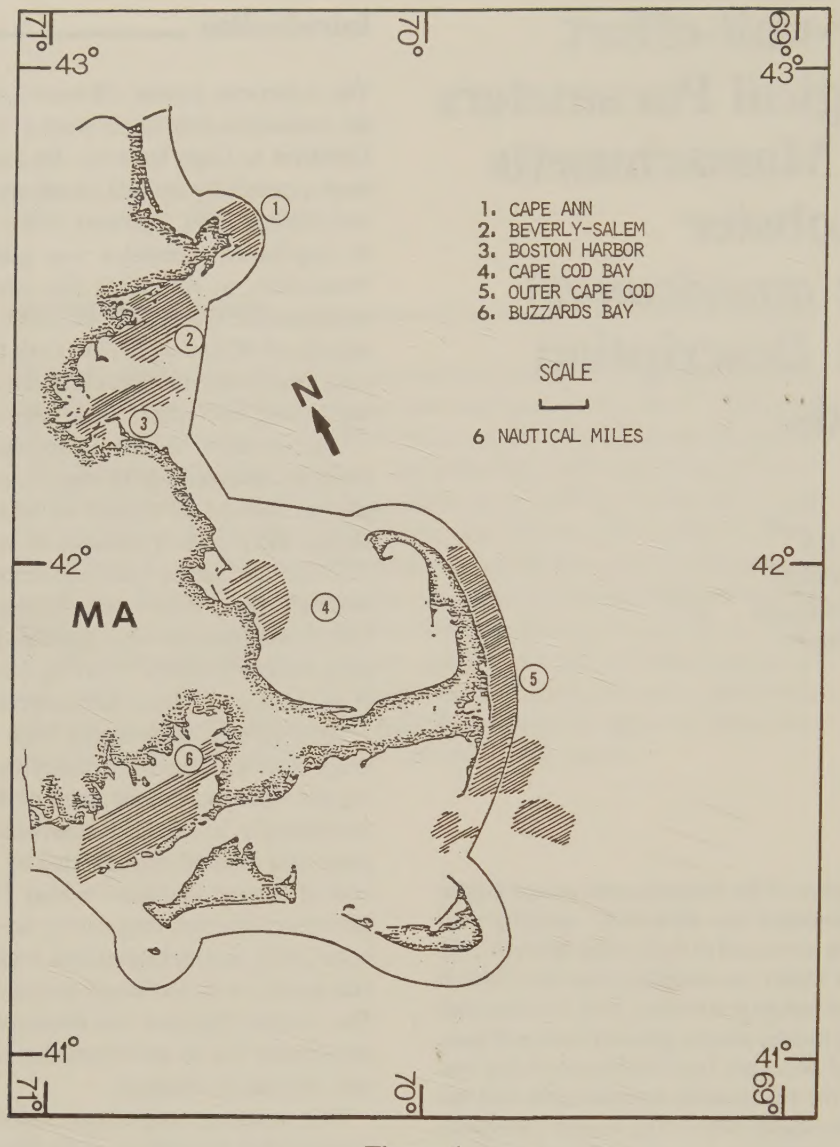

Figure 1
Map of Massachusetts coast showing hatch-marked sampling regions and territorial boundary line.

Sampling

Sampling of coastal waters was accomplished by monitoring catches during normal lobstering operations of volunteer commercial lobstermen in each designated region. Multiple lobstering operations were observed to reduce bias from varying degrees of lobstering skill and to enhance areal coverage. Five lobstermen were monitored in the southern Gulf of Maine regions (Cape Ann south through Cape Cod Bay), three in the outer Cape Cod region, and three in Buzzards Bay. Trap-sampling events were day trips, conducted at least monthly per region (except when manpower limitations precluded effort or cooperating lobstermen were not operating) during the major lobstering season, May-November. Sampling effort during the study period increased with manpower availability. In 1981, 36 sampling trips were conducted during which 12,392 lobster were sampled from 5,736 trap hauls. In 1986, 82 sampling trips were made during which 40,114 lobster were sampled from 14,799 trap hauls.

Sea samplers used portable cassette tape recorders to record the following parameters: **1** Carapace length (CL) to the nearest mm (to the nearest 0.1 mm between 80.5 and 81.0 mm in order to establish minimum legal size which was 81 mm CL during the study period); **2** sex; and **3** condition, including degree of shell hardness, culls (lobster with missing or regenerating claws), mortality, and presence of extruded ova on females (ovigerous). Catch in number of lobster, number of trap hauls, and set-over-days were also recorded. Studies of maturity, morphometrics, and weight-length relationship (g/mm CL) were accomplished with samples collected at sea and at commercial lobster dealerships.

Analytical procedure

Data were computer coded and keypunched for analysis on the Woods Hole Oceanographic Institution's computer system (Digital Equipment Corp. VAX-11/780). A computer auditing process was used to detect keypunch and recording errors, and statistical analyses were performed with SPSS (Nie 1983) and SAS (SAS Inst. 1985) statistical subprograms.

An areal and temporal data-weighting scheme was incorporated into analytical software because parameter means exhibit significant regional and monthly variations. As a result, each month's data contribute equally to regional parameter means which are weighted by area in square nautical miles when generating coastwide means.

Unless specified otherwise, the terms "legal" or "legal-sized" lobster include all lobster in the carapace-length category ≥81 mm. The non-ovigerous segment of this category is analyzed separately and referred to as "marketable lobster." The sublegal length category includes all lobster <81 mm CL.

Data on lobster landings and effort (number of traps fished) are derived from lobstermen's catch reports compiled annually by the Commercial Fisheries Statistics Project of the Massachusetts Division of Marine Fisheries.

Since current management strategy stresses uniform coastwide regulations, all data are grouped for a coastwide analysis. However, two factors mandate a regional data treatment as well: the uniqueness of the Massachusetts coastline with its role in providing a temperature barrier at the southern end of the Gulf of Maine which profoundly affects many marine species (Colton 1964), and the influence of offshore lobster stocks on the inshore resource.

Results

Relative abundance

Immersion-time standardization Indices of relative abundance traditionally used to assess the lobster fishery include catch per trap haul (CTHAUL) and catch per trap haul/set-over-day (CTHSOD). Thomas (1973) reported CTHAUL as unreliable due to its insensitivity to seasonal changes in catchability and emphasized the importance of incorporating immersion time (gauged by set-over-days) into the index, since catch varies with fishing time. Consequently, CTHAUL is useful only in assessing annual abundance trends if immersion time does not vary considerably. CTHSOD represents an improvement over CTHAUL because of its temporal weighting function; however, this index is unrealistic because catch does not increase in direct proportion to immersion time.

The relationship between catch and immersion time was investigated for American lobster trap fisheries (Thomas 1973, Skud 1979, Fogarty and Borden 1980, Auster 1985). These studies concluded that catch increased with immersion time at a decreasing rate toward an asymptote. This declining fishing efficiency over time is a function of reduced entry due to bait breakdown, trap saturation, escapement, or progressive exploitation of available lobster. Miller (1983) reviewed previous efforts to model this relationship in trap fisheries for other species as well.

Gulland (1955) derived a nonlinear regression model to describe the relationship between catch and immersion time:

$$C_s = C_\infty(1-e^{-Rs})$$

where C_s is the catch on day s, C_∞ is the asymptotic catch, and R is the capture rate. Caddy (1977) recommended the use of this model to standardize effort to a common immersion time. Miller (1983) regarded it as a widely accepted model.

To establish a relationship between catch and immersion time for use in our analyses, we used 1985-86 CPUE data (no. lobster) collected from the Cape Ann region. These data were advantageous because of the large sample size (observations from 6,167 trap hauls), which included a wide range of immersion times, and because all data were collected from a single lobsterman, thereby eliminating variability attributable to fishing skill.

Only catch rates for marketable lobster were analyzed. Sublegals were excluded in order to avoid excessive variation in catch rates resulting from escapement through vents, variable vent number, and location. Data were partitioned by season: Spring (May, June), summer (July, Aug., Sept.), and autumn (Oct., Nov.). The relationship between CTHAUL and immersion time was expressed by Gulland's (1955) non-linear regression model (Fig. 2). Generally, catch increased over time at a decreasing rate toward an asymptote. The relationship for spring data showed a longer time-period before an asymptote was reached than for summer and autumn data. The high catch rates and shorter time to an asymptote observed during summer and autumn probably reflect the shorter bait-attraction time due to bait breakdown and the greater availability of legal lobster due to recruitment from the molt. The spring relationship probably resulted from the effect of cold water temperature in extending bait life and reducing lobster activity. These factors would be expected to result in poorer catch rates. The reduced availability of legal lobster due to fishing pressure is another factor which may cause catch rates to decline.

In order to correct for variable immersion time, we adapted Sinoda and Kobayasi's (1969) approach:

$$C'_s = C_s(1-e^{-Rs^*}/1-e^{-Rs})$$

where C'_s is the adjusted catch at day s, C_s is the empirical catch/trap haul on day s, R is the capture rate, and s^* is the standard immersion time (modal or mean immersion time). The ratio term is an estimate of fishing power and serves as a correction factor for set-over-days.

Effort was standardized to our survey modal value of 3, whereby catches of traps hauled following a 3-day immersion were assigned the immersion correction factor of 1.0. Immersion times greater than or less than 3 days were

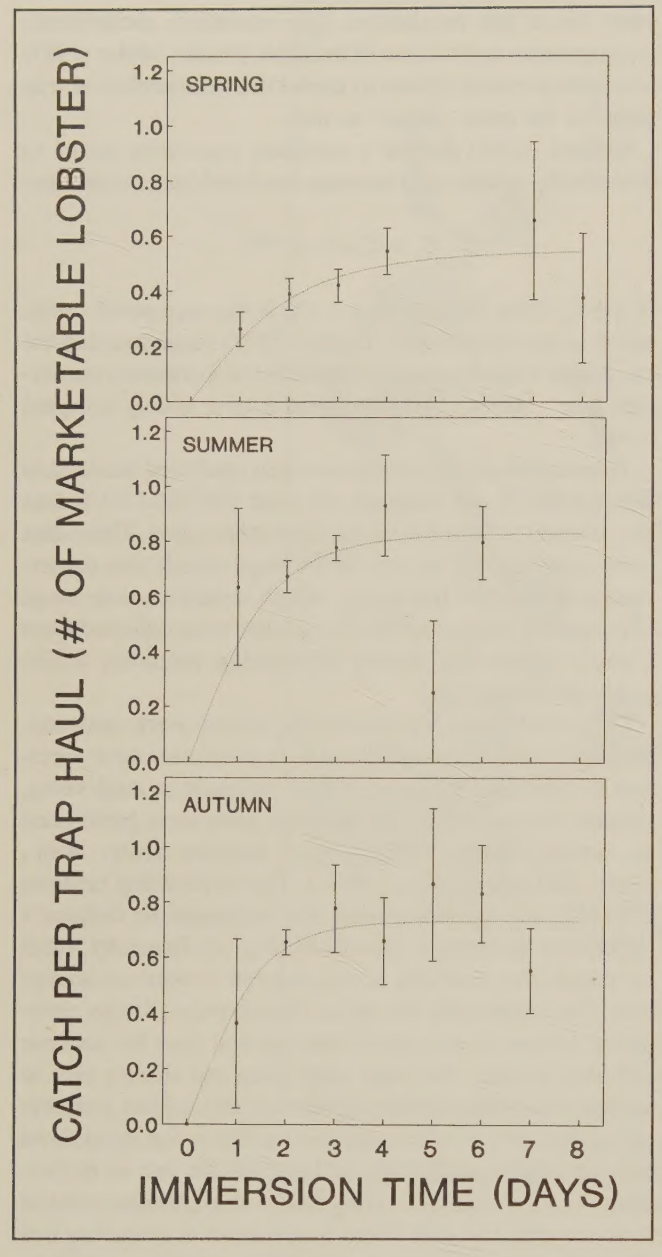

Figure 2

Relationship between predicted American lobster CTHAUL (catch/trap haul) and immersion time (dotted line), with observed CTHAUL means and 95% confidence intervals.

adjusted accordingly (Table 1). These corrected estimates of immersion time were used to calculate an adjusted CTHSOD index for marketable lobster which we labeled CTH'_3 (CTHAUL standardized to 3 set-over-days, Table 2).

The new index reduces the variability in annual indices (relative to annual changes in landings) which is evident in the conventional CTHSOD time-series (Table 3) and tracks the landings' trend for territorial waters very well (Fig. 3). Its 6-year trend is similar to that of CTHAUL (Table 4) only because the mean annual immersion times for the 1981-86 sampling period were similar, ranging from 3.3987

Table 1

Seasonal estimates of regression model coefficients, predicted CTHAUL (catch/trap haul in numbers of lobster), and soak-time correction factors for Massachusetts commercial lobster data.

	Spring		Summer		Fall	
C_∞	0.54602		0.83002		0.73470	
(SE)	(0.05424)		(0.04406)		(0.04646)	
R	0.60831		0.88977		1.11799	
(SE)	(0.15038)		(0.19040)		(0.30781)	
Day	Predicted CTHAUL	Corr. factors	Predicted CTHAUL	Corr. factors	Predicted CTHAUL	Corr. factors
1	0.24883	0.54333	0.49809	0.63313	0.49450	0.69744
2	0.38427	0.83905	0.68998	0.89318	0.65617	0.92545
3	0.45798	1.00000	0.77250	1.00000	0.70903	1.00000
4	0.49810	1.08760	0.80639	1.04388	0.72630	1.02437
5	0.51994	1.13528	0.82032	1.06190	0.73196	1.03243
6	0.53182	1.16123	0.82603	1.06930	0.73380	1.03495
7	0.53829	1.17536	0.82838	1.07234	0.73441	1.03580

Table 2

CTH'_3 (catch/trap haul in numbers of lobster standardized to 3 set-over-days), statewide and by region, for all marketable American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	0.767	0.785	0.803	0.696	0.825	0.816
Cape Ann	0.732	0.808	0.624	0.663	0.634	0.699
Beverly-Salem	0.934	0.898	0.881	0.835	0.663	0.496
Boston Harbor	—	—	—	1.108	1.254	1.096
Cape Cod Bay	0.710	0.776	0.680	0.479	0.716	0.822
Outer Cape Cod	0.808	0.824	0.765	0.598	0.856	0.811
Buzzards Bay	0.611	0.571	1.110	0.870	0.953	0.907

Table 3

CTHSOD (catch/trap haul per set-over-day in numbers of lobster), statewide and by region, for all marketable American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	0.249	0.309	0.302	0.238	0.284	0.263
Cape Ann	0.181	0.349	0.304	0.289	0.238	0.267
Beverly-Salem	0.305	0.368	0.397	0.291	0.197	0.146
Boston Harbor	—	—	—	0.362	0.467	0.367
Cape Cod Bay	0.287	0.364	0.285	0.178	0.280	0.275
Outer Cape Cod	0.125	0.146	0.138	0.113	0.180	0.130
Buzzards Bay	0.202	0.190	0.320	0.314	0.327	0.356

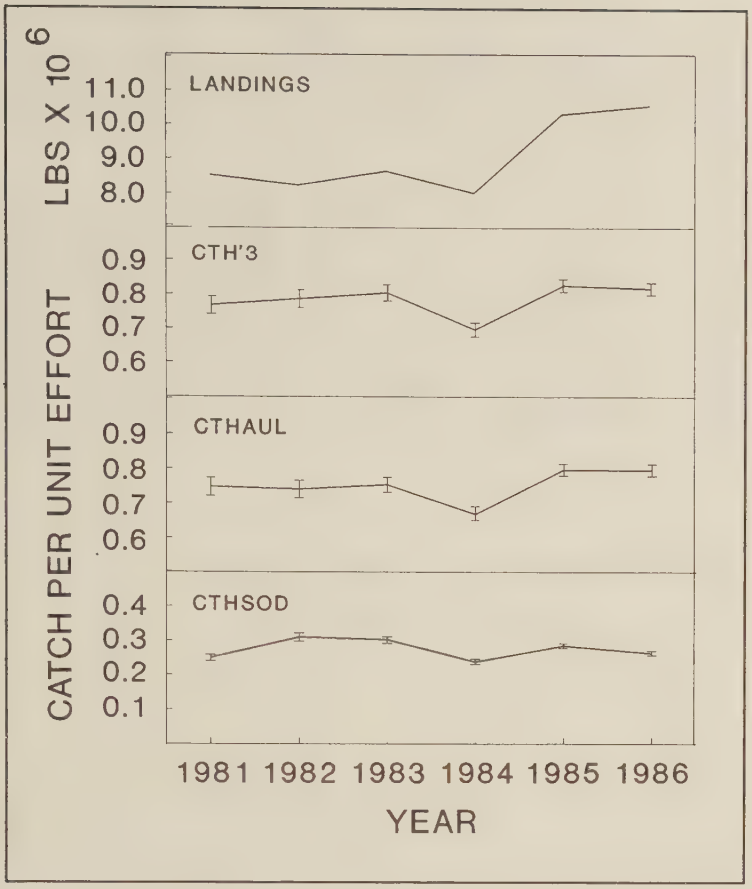

Figure 3
Commercial American lobster landings and CPUE indices from Massachusetts territorial waters, 1981-86. CTHAUL = catch/trap haul; CTHSOD = catch/trap haul per set-over-day; CTH'_3 = CTHAUL standardized to 3 set-over-days.

Table 4
CTHAUL (catch/trap haul in numbers of lobster), statewide and by region, for all marketable American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	0.747	0.740	0.753	0.668	0.796	0.795
Cape Ann	0.759	0.723	0.504	0.578	0.596	0.660
Beverly-Salem	0.884	0.857	0.793	0.780	0.661	0.494
Boston Harbor	—	—	—	1.107	1.181	1.071
Cape Cod Bay	0.658	0.677	0.617	0.446	0.666	0.797
Outer Cape Cod	0.887	0.896	0.811	0.650	0.896	0.859
Buzzards Bay	0.610	0.578	1.116	0.821	0.938	0.835

to 3.7489. Greater benefits of enhanced data comparability and accuracy of trends were realized in the smaller regional data sets where annual mean immersion times sometimes differed substantially. Consequently, this analysis is an important adjunct to small-scale commercial trap-sampling programs in which the mean immersion time sampled is likely to exhibit annual variability.

An analysis of the CTH'_3 index for marketable lobster during the 6-year study period did not indicate significant differences (based on presence or absence of overlap of 95% confidence intervals) in the 1981-83 indices, but a statistically significant decline occurred in 1984. This was followed by a significant increase in 1985, with no statistical difference in 1986.

Catches of sublegal lobster are affected by both soak time and escapement through vents; consequently, soak-time standardization modeling for this size group would require different assumptions. Sublegal lobster catch rates were therefore limited to conventional CTHSOD (Table 5) and CTHAUL (Table 6) indices which generally increased through 1983, significantly declined in 1984, then increased again through 1986.

Commercial landings Historical landings data provide a perspective on the current condition of the fishery and support recent catch-rate trends. Annual Massachusetts coastal landings (excludes data from offshore fishery), available only in number of lobster, generally declined between 1888 (1,740,850) and 1917 (402,469), then gradually increased through 1921 (1,618,988; Fig. 4). Subsequent landings, available only in pounds, increased through 1947 (2,341,882 to 3,663,363 lbs), but were relatively stable thereafter through 1974. Major increases occurred between 1975 (5,172,545 lbs) and 1986 (12,580,793 lbs).

These trends in landings were primarily a reflection of nominal fishing effort (total traps fished). Reported effort averaged below 20,000 traps through 1918; 30,000-40,000 traps through 1929; 60,000 traps during 1930-40; then

Table 5

CTHSOD (catch/trap haul per set-over-day in numbers of lobster), statewide and by region, for all American lobster <81 mm CL, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	0.580	0.672	0.718	0.521	0.647	0.700
Cape Ann	0.067	0.109	0.586	0.450	0.395	0.474
Beverly-Salem	0.708	0.711	1.263	0.948	0.833	0.801
Boston Harbor	—	—	—	0.901	1.162	1.138
Cape Cod Bay	0.710	1.013	0.639	0.322	0.594	0.551
Outer Cape Cod	0.037	0.024	0.038	0.033	0.035	0.027
Buzzards Bay	0.787	0.620	0.638	0.785	0.848	1.312

Table 6

CTHAUL (catch/trap haul in numbers of lobster), statewide and by region, for all American lobster <81 mm CL, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	1.473	1.401	1.624	1.389	1.705	1.899
Cape Ann	0.256	0.199	1.044	0.909	1.031	1.126
Beverly-Salem	1.855	1.713	2.526	2.504	2.567	2.435
Boston Harbor	—	—	—	2.773	3.038	3.314
Cape Cod Bay	1.544	1.680	1.345	0.825	1.337	1.512
Outer Cape Cod	0.233	0.145	0.210	0.189	0.160	0.161
Buzzards Bay	2.381	1.916	2.316	1.965	2.452	3.118

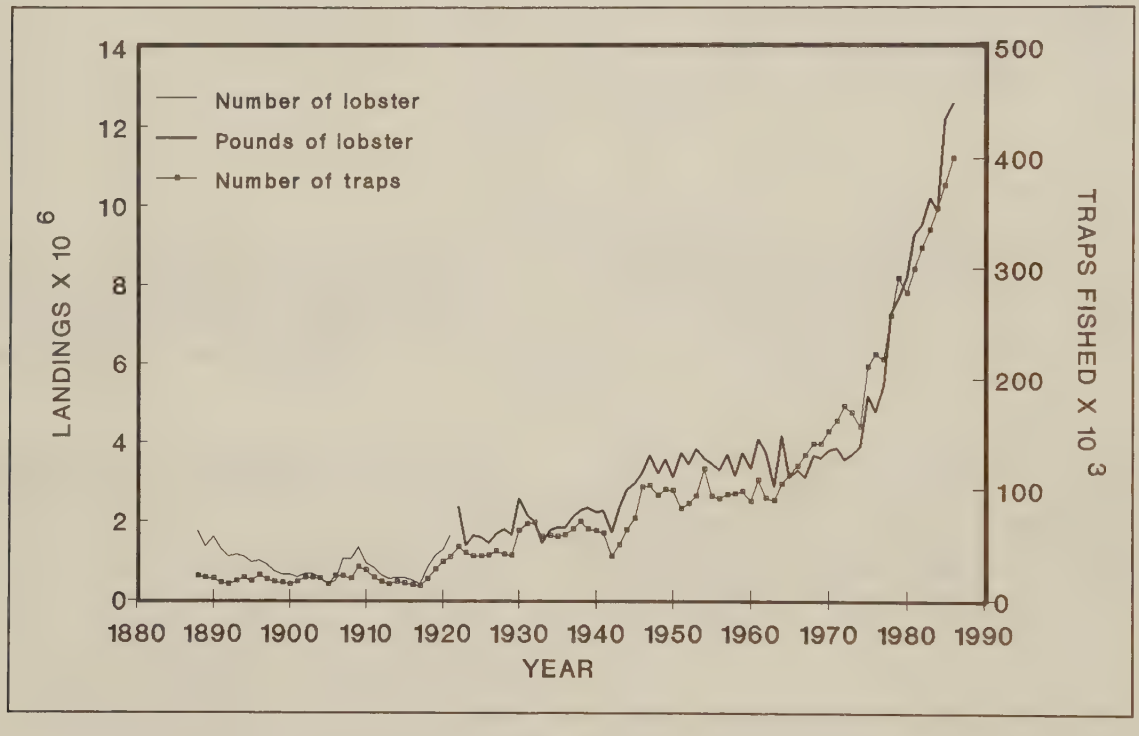

Figure 4

Historical American lobster landings and effort data for Massachusetts, 1888-1986.

100,000 traps through 1964. From 1965 to 1986 the number of traps increased from 100,000 to ~400,000 traps.

Although increased fishing effort has resulted in steadily increasing landings, the average annual pounds per trap (annual landings/total traps fished) declined between the mid-1960s and mid-1970s (Fig. 5). It is conceivable that this may have resulted from a saturation of easily accessible, coastal lobster habitat with traps. Nevertheless, the annual average pounds/trap increased between the late 1970s and 1986. This trend is consistent with CTH'_3 data for the 1981-86 period.

Increases in CPUE between 1976 and 1986 may have been caused by several factors acting in concert:

1 Expansion of lobstermen's territories to deeper, relatively less-exploited habitat to avoid competition.

2 Improved fishing efficiency due to the advent of LORAN C and color depth finders and their increased use on lobster boats. These assist in relocating prime lobstering grounds in deeper, more offshore waters where landmark relocation is not possible.

3 Enhanced lobster larval survival due to favorable environmental conditions (i.e., warming trend through late 1970s) may have increased population size. Temperature is also an important factor controlling molting (Campbell 1983). Optimal water temperature will enhance the proportion of lobster molting and maximize legal catch.

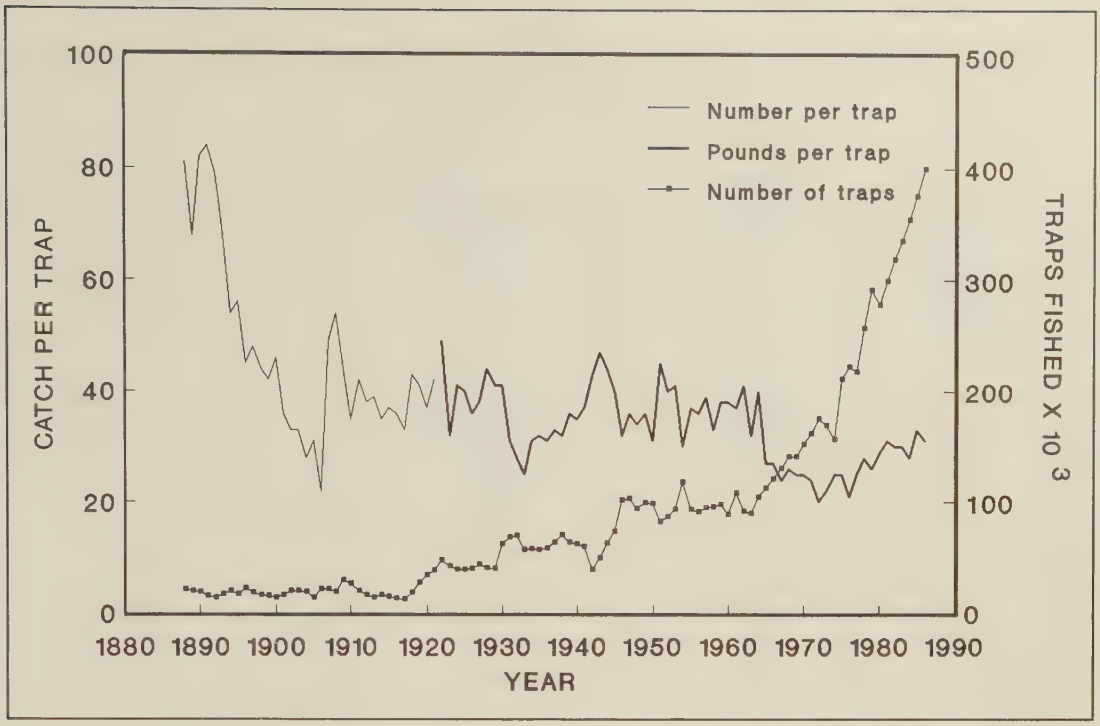

Figure 5
Historical American lobster landings and catch/trap data for Massachusetts, 1888-1986.

4 Juvenile lobster survival may have been aided by the installation of escape vents in traps mandated by a 1977 Massachusetts regulation. Escape vents also enhance the catch of legal-sized lobster, presumably due to an inverse relationship between crowding and probability of entry (Krouse and Thomas 1975, Fair and Estrella 1976, Krouse 1978, Nulk 1978, Pecci et al. 1978, Fogarty and Borden 1980).

Total lobster landings from all lobster harvesting states also increased between the late 1970s and 1986 (Anonymous 1988). These increases cannot be attributed to greater fishing effort alone. In the Canadian Maritimes, where trap limits and a license moratorium (including a license buy-back system) have been enforced for years, landings have also increased. Landings there have doubled, and in some areas have increased five-fold, since 1981 (D.S. Pezzack, Dep. Fish. Oceans, Halifax, Nova Scotia, Canada B3J 2S7, pers. commun., June 1988).

Mortality estimates

Estimates of total instantaneous mortality (Z) and total annual mortality ($A = 1 - e^{-Z}$) were computed by two methods (which produce extremes in the possible range of estimates). The method of Gulland (1969) requires computing the slope of the regression line of numbers at estimated age—15% molt groups calculated from mean carapace-length increases attained from molting (Fair 1977), 14% for Buzzards Bay (Estrella, unpubl. data)—plotted in the natural log. Beverton and Holt's (1956) process employs von Bertalanffy growth equation parameters ($K = 0.0634$, $L_\infty = 253$ mm; Fair 1977) and mean and minimum length of exploitable sizes:

$$Z = K(L_\infty - l)/(l - l_c)$$

where K = growth rate constant,
L_∞ = asymptotic length,
l = mean length of exploitable sizes, and
l_c = minimum exploitable size.

Total annual mortality estimates (A), when computed by the method of Gulland (1969), were generally high. Six-year means ranged from 85% (Cape Ann) to 94% (Boston Harbor) in Gulf of Maine regions, with 97% in Buzzards Bay and 36% off outer Cape Cod (Table 7). Estimates computed by the method of Beverton and Holt (1956) ranged from 74% (Cape Ann) to 84% (all others) in Gulf of Maine regions, with 91% in Buzzards Bay and 42% off outer Cape Cod.

Results of Gulland's method tend to be slightly higher than those of Beverton and Holt's for all regions except outer Cape Cod. Considering the high level of effort in most of the inshore area, the higher estimates seem more realistic. Mortality estimates have increased over time in response to escalated fishing effort. The 1981-86 mean Cape Cod Bay estimates of total instantaneous mortality and total annual mortality were $Z = 2.55$ and $A = 92\%$, respectively, when calculated by Gulland's procedure. These values were slightly higher than 1970-76 means calculated from length-

Table 7

Total instantaneous (Z) and total annual percent (A) mortality estimates of American lobster statewide and by region, Massachusetts coastal waters, 1981-86.

	1981		1982		1983		1984		1985		1986		Mean	
	Gulland (1969)	Beverton and Holt (1956)	Gulland (1969)	Beverton and Holt (1956)	Gulland (1969)	Beverton and Holt (1956)	Gulland (1969)	Beverton and Holt (1956)	Gulland (1969)	Beverton and Holt (1956)	Gulland (1969)	Beverton and Holt (1956)	Gulland (1969)	Beverton and Holt (1956)
State	1.58	1.35	1.72	1.45	1.66	1.39	1.66	1.41	1.76	1.47	1.80	1.49	1.70	1.43
	79%	74%	82%	77%	81%	75%	81%	76%	83%	77%	84%	78%	82%	76%
Cape Ann	1.65	1.32	2.18	1.39	1.72	1.35	1.92	1.52	1.94	1.33	2.03	1.32	1.91	1.37
	81%	73%	89%	75%	82%	74%	85%	78%	86%	74%	87%	73%	85%	75%
Beverly-Salem	1.97	1.59	2.15	1.70	2.41	1.85	2.71	1.78	3.64	1.96	3.60	1.99	2.75	1.81
	86%	80%	88%	82%	91%	84%	93%	83%	97%	86%	97%	86%	94%	84%
Boston Harbor	—	—	—	—	—	—	2.52	1.82	3.59	1.75	2.60	1.92	2.90	1.83
	—	—	—	—	—	—	92%	84%	97%	83%	93%	85%	94%	84%
Cape Cod Bay	2.53	1.64	2.69	1.92	2.42	1.72	2.52	2.07	2.31	1.88	2.83	1.92	2.55	1.86
	92%	81%	93%	85%	91%	82%	92%	87%	90%	85%	94%	85%	92%	84%
Outer Cape Cod	0.43	0.54	0.46	0.55	0.42	0.53	0.33	0.52	0.52	0.57	0.51	0.55	0.44	0.54
	35%	42%	37%	42%	34%	41%	28%	41%	41%	43%	40%	42%	36%	42%
Buzzards Bay	3.02	2.97	3.00	2.53	8.64	2.26	3.14	2.21	3.55	2.36	3.71	2.41	4.18	2.46
	95%	95%	95%	92%	99%	90%	96%	89%	97%	91%	98%	91%	98%	91%

frequency data by Fair (1977) for the same region and by the same method, $Z = 2.15$ and $A = 88\%$. Coastwide annual mean estimates of Z gradually increased during the 1981-86 study period.

Estimates of fishing mortality (F) were calculated by Cohort Analysis (Pope 1972) which assumes a von Bertalanffy growth curve. Resulting estimates of F plus an assumed natural mortality (M) of 0.15 (Fair 1977) approximate estimates of Z calculated by the Beverton and Holt technique.

Weighted average estimates of F (weighted by 5-mm size frequencies) from Cohort Analysis were:

Statewide	1.27
Cape Ann	1.22
Beverly-Salem	1.93
Boston Harbor	1.80
Cape Cod Bay	1.70
Outer Cape Cod	0.47
Buzzards Bay	2.11

Survey size-frequency data (all lobster ≥81 mm CL) were expanded on the basis of total landings from commercial lobstermen's catch reports. The population of legal-sized lobster in the territorial sea during the 1986 season was then calculated by Cohort Analysis and estimated to be 15,400,000 (Table 8).

Total mortality rates increased only slightly during the 6-year study period; however, significant changes in F can affect yield. These yield changes can be predicted using $F\Delta T$ values obtained from Cohort Analysis (Jones 1974). Results indicate that the current exploitation rates in our coastal regions are so high that only minimal changes in landings would result from substantial changes in F (Table 9). The exception is the relatively less-exploited outer Cape Cod region.

Exploitation rate

Rates of exploitation ($u = FA/Z$, the fraction of the population removed by fishing) and exploitation ratios ($E = F/Z$, the proportion of fishing deaths to all deaths) were calculated with 1986 data. These statistics were estimated in two ways. First, they were computed with A and Z values from the Beverton and Holt (1956) methodology and F values derived from Cohort Analysis (because all incorporate von Bertalanffy parameters); and, second, with A and Z values from Gulland (1969) and F values derived by assuming $M = 0.15$:

	Beverton and Holt (1956)		Gulland (1969)	
	u	E	u	E
Statewide	0.66	0.85	0.77	0.92
Cape Ann	0.67	0.92	0.81	0.93
Beverly-Salem	0.83	0.97	0.93	0.96
Boston Harbor	0.80	0.94	0.88	0.94
Cape Cod Bay	0.75	0.89	0.89	0.95
Outer Cape Cod	0.36	0.85	0.28	0.71
Buzzard Bay	0.80	0.88	0.94	0.96

These indices reflect the substantial impact of fishing on the lobster resource. Intense fishing effort removes the opportunity for individual lobster to grow to large sizes. This effect on size can be described with an additional index which

Table 8

Cohort analysis of 1986 American lobster size-frequency data expanded to total Massachusetts landings.

Length group	No. landed	No. in sea	Mean no.	F/Z	$Z\Delta T$	$F\Delta T$	Z	ΔT	F
166.0---171.0	0.503E+03	0.640E+03							
161.0---166.0	0.545E+03	0.131E+04	0.937E+03	0.810	0.718	0.582	0.790	0.909	0.640
156.0---161.0	0.152E+04	0.310E+04	0.208E+04	0.847	0.859	0.728	0.982	0.875	0.832
151.0---156.0	0.124E+04	0.481E+04	0.389E+04	0.727	0.439	0.319	0.549	0.801	0.399
146.0---151.0	0.223E+04	0.775E+04	0.617E+04	0.760	0.477	0.362	0.624	0.764	0.474
141.0---146.0	0.299E+04	0.118E+05	0.963E+04	0.740	0.419	0.310	0.577	0.727	0.427
136.0---141.0	0.642E+04	0.198E+05	0.155E+05	0.798	0.520	0.415	0.743	0.700	0.593
131.0---136.0	0.108E+05	0.333E+05	0.260E+05	0.806	0.518	0.417	0.772	0.671	0.622
126.0---131.0	0.274E+05	0.653E+05	0.475E+05	0.855	0.674	0.576	1.032	0.652	0.882
121.0---126.0	0.303E+05	0.103E+06	0.828E+05	0.798	0.458	0.366	0.743	0.617	0.593
116.0---121.0	0.468E+05	0.162E+06	0.130E+06	0.801	0.448	0.359	0.755	0.594	0.605
111.0---116.0	0.778E+05	0.257E+06	0.206E+06	0.815	0.464	0.378	0.810	0.573	0.660
106.0---111.0	0.139E+06	0.424E+06	0.334E+06	0.834	0.500	0.417	0.902	0.555	0.752
101.0---106.0	0.244E+06	0.713E+06	0.556E+06	0.845	0.520	0.439	0.969	0.537	0.819
96.0---101.0	0.254E+06	0.103E+07	0.864E+06	0.792	0.371	0.294	0.722	0.515	0.572
91.0--- 96.0	0.118E+07	0.233E+07	0.160E+07	0.905	0.814	0.736	1.572	0.518	1.422
86.0--- 91.0	0.309E+07	0.571E+07	0.377E+07	0.915	0.895	0.819	1.764	0.507	1.614
81.0--- 86.0	0.401E+07	0.103E+08	0.777E+07	0.878	0.587	0.516	1.233	0.476	1.083
Total	0.912E+07		0.154E+08					Wtd. avg. F:	1.271

Table 9

Prediction of the percent change in landings of American lobster at various percent changes in fishing mortality (F), Massachusetts coastal waters, 1986.

	Percent change in F									
	−50	−40	−30	−20	−10	+10	+20	+30	+40	+50
Cape Ann	7.24	7.20	4.58	2.91	1.38	−1.31	−2.44	−3.53	−4.40	−5.45
Beverly-Salem	8.27	7.10	5.43	3.58	1.79	−1.60	−3.33	−4.69	−5.99	−7.22
Boston Harbor	3.88	4.63	4.09	2.95	1.48	−1.51	−2.99	−4.36	−5.70	−6.83
Cape Cod Bay	9.86	7.87	5.69	3.61	1.71	−1.56	−2.99	−4.39	−5.60	−6.75
Outer Cape Cod	21.87	17.06	12.11	7.51	3.45	−3.04	−5.42	−7.40	−9.04	−10.54
Buzzards Bay	7.62	7.00	5.55	3.78	1.92	−1.81	−3.64	−5.18	−6.73	−8.29

is easily computed by expressing the number of lobster in the recruit molt group, 81-93 mm CL, as a percentage of the total number of legal-sized lobster. This "fishing pressure index" was high during the 6-year study period (Table 10). Approximately 87-98% of the lobster landed in all inshore regions, except one, were captured shortly after molting beyond the legal size limit of 81 mm CL. Fishing-pressure indices varied from 38 to 48% between 1981 and 1986 for the outer Cape Cod region, where a large offshore migrant group dominates catches. Buzzards Bay exhibited the highest indices, which varied from 94 to 98% during the study period.

A slight increasing trend in the 6-year time-series of coastwide fishing-pressure indices was discernible (Table 10). Furthermore, a comparison of recent and 30-year-old size-frequency data revealed the effect of escalated fishing effort. Length-frequency data collected July-September 1957

Table 10

Fishing-pressure indices (% of all legal-sized American lobster in recruit molt group), statewide and by region, commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	86	87	86	86	88	88	87
Cape Ann	91	92	87	89	87	87	89
Beverly-Salem	89	92	94	88	96	96	92
Boston Harbor	—	—	—	93	94	96	95
Cape Cod Bay	90	93	92	94	93	94	93
Outer Cape Cod	46	43	42	38	48	46	44
Buzzards Bay	98	96	96	94	96	97	96

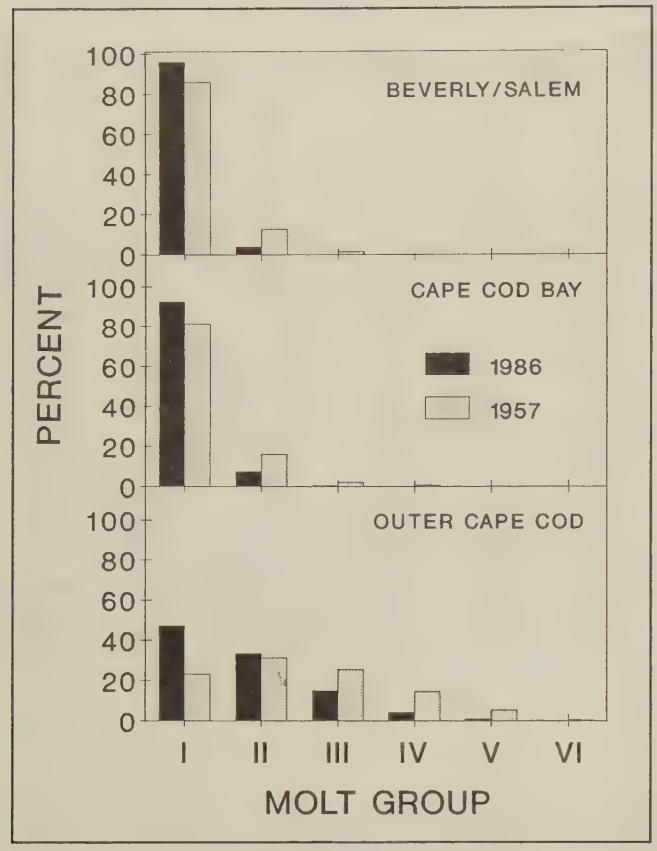

Figure 6

Comparison of 1957 and 1986 marketable American lobster size-frequency data from three coastal Massachusetts regions by 15% molt groups: I 81-93 mm, II 94-108 mm, III 109-125 mm, IV 126-145 mm, V 146-168 mm, VI 169-194 mm.

by sea-sampling commercial traps from three coastal Massachusetts regions were compared with similarly collected 1986 data from the same months and approximate locations (Fig. 6). Size frequencies from Beverly-Salem, Cape Cod Bay, and outer Cape Cod regions were analyzed by 15% increments. A 2-year comparison of group frequencies with the chi-square test demonstrated that annual size frequencies were significantly different for each of these regions ($P<0.01$). This analysis by molt group clearly demonstrates that larger lobster comprised a greater percentage of the catch in 1957 than in 1986.

The prevalence of larger lobster in 1957 is indicative of a lower level of fishing pressure than in recent years, with 95,209 traps reportedly fished and 3,679,953 lbs of lobster landed. By contrast, in 1981 licensed lobstermen reported fishing 299,368 traps and landing 9,282,695 lbs (landward of long. 69°W. and lat. 41°N.). In 1986, a total of 399,808 traps reportedly captured 12,580,793 lbs. The mean pounds/pot index declined from 39 in 1957 to 31 during 1981-86. The pounds/pot/fishermen also declined from 0.0227 in 1957 to 0.0215 in 1981 and 0.0208 in 1986.

Carapace length

Annual mean carapace lengths were calculated by region and regions combined (Tables 11-14). Lobster from Buzzards Bay averaged smaller in size than lobster from all other regions sampled, while those from the outer Cape Cod region averaged largest (Duncans Multiple Range Test, $P=0.05$). Means from southern Gulf of Maine regions (Cape Ann, Beverly-Salem, Boston Harbor, and Cape Cod Bay) were intermediate and similar to one another. Buzzards Bay is comparable to western Long Island Sound in warm average water temperature and constricted access to outer coastal waters. Its lobster size-distribution is similar to that described by Briggs and Mushacke (1979) for the Sound. The Buzzards Bay lobster fishery is almost entirely dependent on new recruits. Recruits from the late spring-early summer molt period are generally depleted by August, particularly in northern Buzzards Bay. At this time, most northern Bay lobstermen undertake alternative fisheries until the autumn molt produces another limited supply of legal-sized lobster.

Table 11

Mean carapace length (mm), statewide and by region, for all American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	81.7	82.1	81.7	81.7	81.6	81.2	81.7
Cape Ann	86.2	86.2	82.1	81.7	82.1	81.8	83.4
Beverly-Salem	78.2	80.0	77.9	78.3	78.2	76.8	78.2
Boston Harbor	—	—	—	79.8	79.2	79.1	79.4
Cape Cod Bay	80.0	79.5	80.0	79.3	79.6	79.7	79.7
Outer Cape Cod	95.5	96.0	95.9	96.5	95.1	95.0	95.7
Buzzards Bay	77.8	78.1	80.1	79.6	78.9	78.4	78.8

Table 12

Mean carapace length (mm), statewide and by region, for all American lobster ≥81 mm sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	88.7	88.2	88.5	88.4	88.1	88.0	90.3
Cape Ann	88.9	88.5	88.7	88.2	88.8	88.9	88.7
Beverly-Salem	87.6	87.2	86.7	86.9	86.4	86.3	86.8
Boston Harbor	—	—	—	86.9	87.0	86.5	86.8
Cape Cod Bay	87.4	86.5	87.1	86.2	86.6	86.5	86.7
Outer Cape Cod	99.1	98.9	99.5	101.1	98.2	98.7	99.2
Buzzards Bay	84.6	85.2	85.7	85.9	85.5	85.4	85.4

Table 13

Mean carapace length (mm), statewide and by region, for all marketable American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	88.5	87.9	88.1	88.2	87.8	87.6	89.4
Cape Ann	88.6	88.3	88.3	87.9	88.4	88.3	86.8
Beverly-Salem	87.6	87.0	86.6	86.9	86.2	86.2	86.7
Boston Harbor	—	—	—	86.8	86.9	86.4	86.7
Cape Cod Bay	87.2	86.4	86.9	86.1	86.4	86.3	86.6
Outer Cape Cod	98.2	97.5	97.4	99.7	97.0	96.3	97.7
Buzzards Bay	84.7	85.2	85.7	85.8	85.2	85.3	85.3

Table 14

Mean carapace length (mm), statewide and by region, for all American lobster <81 mm sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	75.8	76.3	76.2	76.1	76.3	76.1	76.1
Cape Ann	78.0	77.7	77.5	77.3	77.6	77.1	77.5
Beverly-Salem	74.3	76.5	74.9	76.1	75.9	74.7	75.4
Boston Harbor	—	—	—	77.1	76.9	76.9	77.0
Cape Cod Bay	76.6	76.4	76.7	75.6	76.1	76.2	76.3
Outer Cape Cod	75.9	76.2	77.1	75.1	76.6	75.9	76.1
Buzzards Bay	75.8	75.5	76.8	76.4	76.1	76.0	76.1

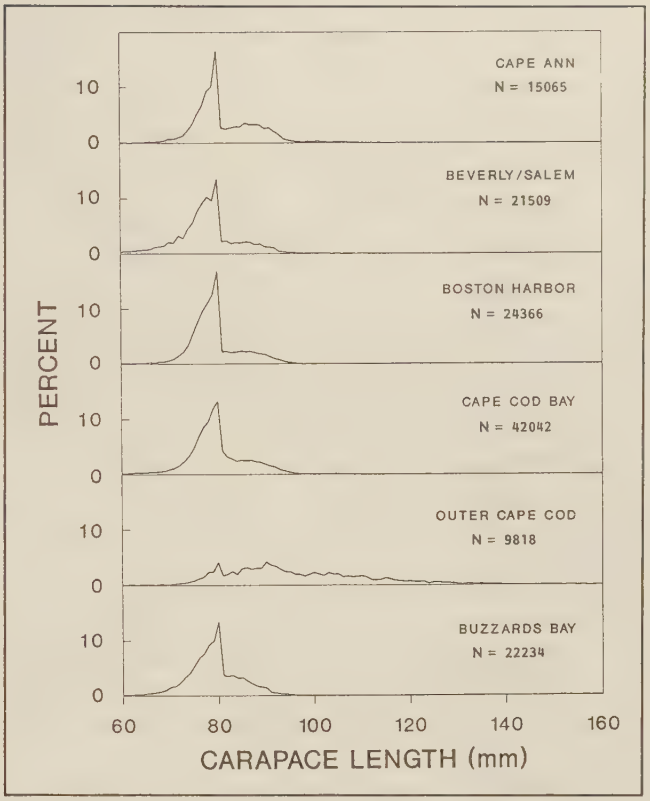

Figure 7

Comparison of 1981-86 summaries of American lobster size-frequency data from six coastal Massachusetts regions.

It is noteworthy that Buzzards Bay exhibited the highest fishing pressure (6-year mean fishing-pressure index of 96%; Table 10) and was also characterized by the smallest mean carapace length of legal-sized lobster (6-year mean 85.4 mm). Few lobster larger than 90 mm were found in this embayment. Krouse (1973) and Fogarty and Borden (1980) observed the same relationship between fishing pressure and size.

The size characteristics of the lobster group off outer Cape Cod were significantly different. Catches in this fishery are seasonally augmented by the shoalward migration of large offshore lobster which exhibit extensive migratory behavior (Morrissey 1971). In addition, numerous tagged lobster from recent Maine and Canadian tagging studies (Campbell 1982) were recaptured in this region. A south-to-southwesterly movement pattern of large mature lobster from Maine into Massachusetts waters was described by Dow (1974).

Inshore-offshore movement of lobster probably occurs in response to changes in water temperature. Cooper and Uzmann (1971) elaborated on the seasonal mixing of inshore and offshore stocks all along the range of the American lobster. Briggs and Mushacke (1980) encountered the greatest number and widest size range of lobster in July and August off the south shore of Long Island and classified this as an offshore size distribution. The offshore influence on Cape Ann lobster is discernible through size-frequency analysis. Of all regions sampled, the percentage of lobster ⩾100 mm CL was greatest off Cape Ann (5.5%) and outer Cape Cod (40.1%; Fig. 7).

There is additional evidence of infiltration of migrating lobster from outside Massachusetts territorial waters. Numerous observations of lobster marked with V-shaped notches in their uropods have been made during the study period off Cape Ann and outer Cape Cod. These lobster are presumed to have migrated from Maine waters where a V-notched female protection program is enforced. This is an industry-sponsored program intended to protect a segment of the brood stock off the coast of Maine.

During commercial lobster-trap sampling off Cape Ann, 3.4%, 3.3%, and 2.2% of the legal-sized females were observed with V- notches during the years 1984-86, respectively. Observations in the outer Cape Cod region totaled 3.1%, 5.8%, and 6.2% for the same time period. All other Massachusetts inshore regions sampled exhibited low percentages (0-0.8). V-notched females were generally large, averaging greater than 100 mm CL.

Geography may be a factor in concentrating migrants off Cape Ann and outer Cape Cod. These regions are adjacent to steeply sloping gradients which lead to a much greater depth range than is available to other, more "sheltered," inshore regions.

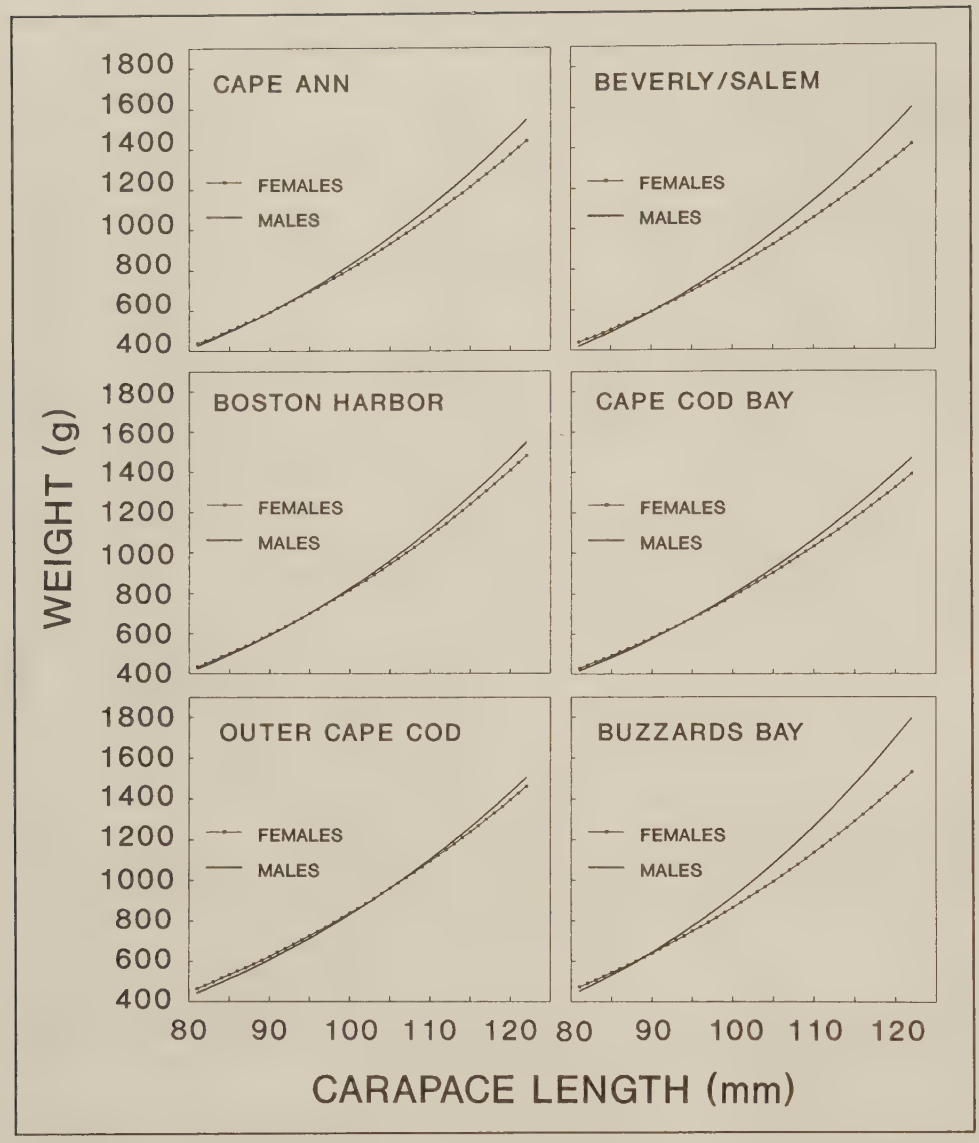

Figure 8
American lobster weight-length relationships by sex and region, from six coastal Massachusetts regions.

Mean carapace lengths for legal and sublegal size groups off Massachusetts were remarkably consistent during the 6-year study period (Tables 12-14). The mean sizes of lobster ⩾81 mm calculated during 1981-86 for Beverly-Salem (86.3 mm), Cape Cod Bay (86.5 mm), and Buzzards Bay (85.4 mm) were similar to those calculated in 1976 by Fair and Estrella (1976) for the same regions (86.9, 87.3, 85.1 mm, respectively). This minimal size variation in recent years is likely due to the recruitment dependency of this intensively exploited fishery. Nearly all lobster landed are those which molted into legal size during their last molt. Consequently, potential variation in mean size from variable year-class strength, and/or magnitude of seasonal inshore migrations of large offshore lobster, is likely to be mitigated by fishing pressure.

Weight-length relationship

In order to determine the weight-length relationship, lobster carapace lengths (mm) and corresponding body weights (g) were collected at dealerships in the six designated coastal regions between 1980 and 1988. Weight and length data were collected throughout the seasons so expected weights-at-length are annual means. Body weight varies seasonally relative to the molt and is usually lower during summer and autumn, following molting, than during winter and spring.

Since lobster larger than 120 mm were rare, only those in the 81-120 mm CL size range, excluding culls, were analyzed, yielding a sample size of 4933 (M 2411, F 2522). A logarithmic transformation of the data was fitted to the equation $W = aL^b$ by the method of least-squares, generating the following relationships:

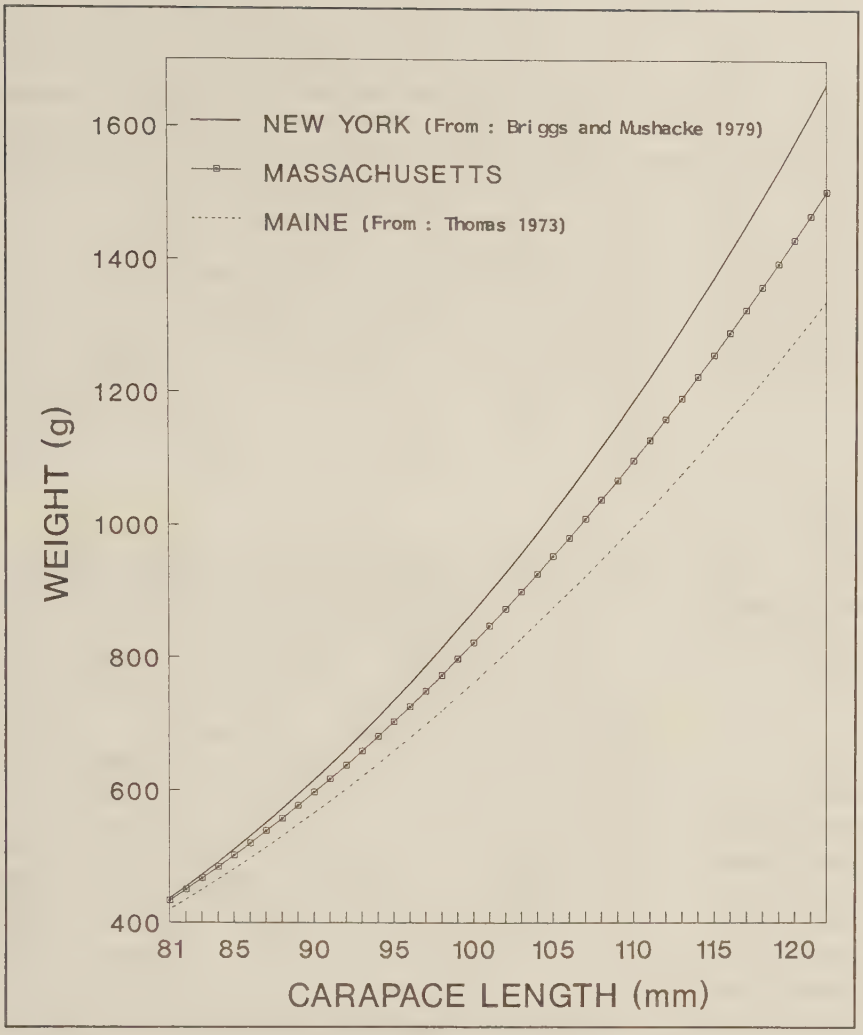

Figure 9
Comparison of American lobster weight-length relationships from New York, Massachusetts, and Maine.

$W = 0.0006920\ L^{3.0374}$ (sexes combined),
$W = 0.0004692\ L^{3.1221}$ (males),
$W = 0.0009490\ L^{2.9687}$ (females).

Analysis of covariance of regression coefficients revealed a highly significant difference between the slopes and/or intercepts of the male and female regression lines for each region and regions combined ($P<0.001$). Covariance analyses of regional regression coefficients produced significant differences among regions for male ($P = 0.001$) and female ($P = 0.001$) data.

When regional data sets were combined, females weighed slightly more than males at each millimeter increment between 81 and 98 mm. At 99 mm and larger, a reversal occurred which was evident at varying sizes in all regional weight-length relationships (Fig. 8). This reversal was probably related to the gradual attainment of sexual dimorphic characteristics with the onset of maturity. Females may gain less weight per molt than males, due to maturity-related changes in physiology and an expenditure of energy toward ovarian development. Female abdomens may broaden at maturity to accommodate egg masses, but it is not clear if increased volume and abdominal surface area are achieved without increased weight. In contrast, the weight gain from increased cheliped size in males is significant.

There is conflicting evidence in the literature regarding a differential weight-length relationship for males and females. Thomas (1973) found no significant difference between male ($N = 336$) and female ($N = 391$) regression lines when investigating the weight-length relationship in Maine lobster. His tests were run on the sublegal-legal size range. Briggs and Mushacke (1979) also found no difference between male ($N = 52$) and female ($N = 52$) lobster weight-length relationships in western Long Island Sound. Their samples ranged from 17 to 118 mm CL. However, Campbell (1983) observed a significant difference ($P<0.01$) between the slopes of male ($N = 135$) and female ($N = 197$) regression lines for lobster (47-144 mm) from Port Maitland, Nova Scotia. Males were heavier than females. Aiken (1980) described a similar relationship for lobster from Lydonia Canyon.

Weight-length relationships (sexes combined) from Maine, Massachusetts, and New York reflect north-south clinal variation (Fig. 9). Lobster weight-at-length increased from

Table 15

Percent of male American lobster, statewide and by region, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	42.0	41.0	41.0	38.0	41.9	40.2	40.7
Cape Ann	42.0	46.0	39.0	35.0	41.2	40.7	40.6
Beverly-Salem	44.0	41.0	51.0	50.0	42.2	50.7	46.5
Boston Harbor	—	—	—	40.0	48.2	40.8	43.0
Cape Cod Bay	39.0	36.0	36.0	36.0	40.6	40.3	38.0
Outer Cape Cod	44.0	46.0	44.0	41.0	45.9	38.1	43.2
Buzzards Bay	43.0	47.0	36.0	34.0	36.2	31.9	38.0

Table 16

Percent of male American lobster ≥81 mm carapace length, statewide and by region, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	44.0	47.0	45.0	41.0	45.6	42.8	44.2
Cape Ann	47.0	51.0	42.0	36.0	44.8	43.6	44.1
Beverly-Salem	47.0	49.0	62.0	59.0	44.3	57.4	53.1
Boston Harbor	—	—	—	45.0	57.6	48.2	50.3
Cape Cod Bay	43.0	45.0	45.0	43.0	47.2	48.6	45.3
Outer Cape Cod	43.0	44.0	41.0	41.0	45.3	36.8	41.8
Buzzards Bay	44.0	48.0	35.0	31.0	32.7	25.9	36.1

north to south. This trend was also evident within Massachusetts coastal waters. Buzzards Bay lobster had greater weights-at-length than those from regions north of Cape Cod ($P<0.01$). The equations from all other Massachusetts regions were similar to one another.

Sex ratio

The coastwide annual percentage of males in the catch ranged from 38 to 42% during the 1981-86 period (Table 15). The percentage of male lobster ≥81mm ranged from 41 to 47%, while that for sublegal males ranged from 36 to 40% (Tables 16 and 17).

Females outnumbered males in nearly all regions during every year of the study period. Chi-square analysis of annual sex ratios indicated that in all cases the ratios differed significantly from 1:1 ($P<0.01$).

A majority of females in the sublegal catch may be attributed to the reduced growth rate of females after the onset of sexual maturity, while the protection of ovigerous females from exploitation would enhance the proportion of females in the legal catch. Saila and Flowers (1965) constructed a model of lobster stock composition and demonstrated the latter to contribute to a higher proportion of females in the legal-size category.

Behavioral segregation by sex may also affect sex ratio. Indications are that sex ratio may vary by depth, with females frequenting deeper water than males (Skud and Perkins 1969, Briggs and Zawacki 1974, Cooper et al. 1975, Briggs and Mushacke 1979). The sublegal sex ratio near Boothbay Harbor, Maine, approximated 50:50 (Krouse 1973, Cooper et al. 1975) while females predominated (M:F = 24:76) in deeper (30-60 m) Maine waters (Cooper et al. 1975).

A sex ratio in favor of males was observed in a mainly sublegal population in a shallow cove in Buzzards Bay (Jelle Atema, Mar. Biol. Lab., Woods Hole, MA 02543, pers. commun., March 1983). This was hypothesized to have been due to mature male competition in deeper water for territory and mating burrows, thereby concentrating sublegal males in shoalwater areas.

Table 17

Percent of male American lobster <81 mm carapace length, statewide and by region, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	40.0	37.0	38.0	36.0	39.6	38.7	38.2
Cape Ann	24.0	30.0	36.0	35.0	38.8	38.8	33.8
Beverly-Salem	43.0	37.0	47.0	47.0	41.6	49.1	44.1
Boston Harbor	—	—	—	38.0	44.6	38.5	40.4
Cape Cod Bay	37.0	33.0	31.0	32.0	37.3	36.0	34.4
Outer Cape Cod	53.0	54.0	55.0	44.0	49.3	44.5	50.0
Buzzards Bay	42.0	47.0	37.0	35.0	37.8	33.9	38.8

Lower proportions of males in the catch of sublegal lobster may also be caused by differential escapement from traps (Fogarty and Borden 1980). Sexual dimorphism in the carapace length-width relationship may be responsible, since carapace width is the critical factor affecting escapement through vents. In order to test this hypothesis, carapace length and corresponding widths were collected through dealer and sea-sampling efforts from 1983 to 1987. A total of 7,417 lobster from six coastal regions were tested. Only lobster with carapace lengths of 69-93 mm were analyzed. This range includes the pre-recruit (69-80 mm) and recruit (81-93 mm) molt groups and encompasses the size range most often encountered in the inshore trap fishery.

Analysis of covariance of regression coefficients indicated no difference between the slopes of length-width relationships for legal-sized females from each of the six regions (Table 18). Tests of elevations of slopes indicated that expected carapace-width means-at-length (y-intercepts) were significantly wider for females ($P<0.01$). No significant difference was found between slopes of sublegal male and female regression equations from all regions except Cape Ann. Sublegal females exhibited a significantly wider carapace width than males ($P<0.01$) in all regions except outer Cape Cod.

Table 18

Results of analysis of covariance of regression coefficients of male and female American lobster carapace length-width relationships, showing significance of differences (*0.05, **0.01, NS = not significant) between slopes and between carapace-width means, and sample size (*N*) by region, Massachusetts coastal waters, 1983-87.

	Legal-sized			Sublegal-sized		
	Slopes	Means	*N*	Slopes	Means	*N*
Cape Ann	NS	**	1,006	*		705
Beverly-Salem	NS	**	1,254	NS	**	780
Boston Harbor	NS	**	635	NS	**	1,280
Cape Cod Bay	NS	**	80	NS	**	125
Outer Cape Cod	NS	**	323	NS	NS	86
Buzzards Bay	NS	**	465	NS	**	678

In Narragansett Bay and Rhode Island Sound, Fogarty and Borden (1980) found that the sex ratio in vented traps was biased toward females. This was attributed to differential escapement by females because of their significantly broader carapace width. However, no significant difference was found between male and female carapace length-width relationships off the coast of Maine (Krouse and Thomas 1975).

Maturity

Female lobster size-at-maturity from five Massachusetts coastal locations was evaluated with the cement-gland staging technique (Aiken and Waddy 1982). Results were compared with ovigerous female size-frequency data from 1981-86 commercial sea-sampling.

From 16 May to 16 June 1986, cement gland development on 2,536 female lobster was assessed in five coastal regions of Massachusetts (Fig. 1): Cape Ann ($n = 634$ lobster), Boston Harbor ($n = 576$), Cape Cod Bay ($n = 656$), outer Cape Cod ($n = 367$), and Buzzards Bay ($n = 303$). Specimens were obtained onboard commercial lobster vessels during our ongoing commercial lobster-trap sampling program, as well as in dealerships where we sampled local fishermen's catches. Pleopods were removed and examined microscopically to stage glandular development; specimens with questionable development were dissected and ovary maturation was assessed according to Aiken and Waddy (1982). Sampling was conducted prior to the spring-summer molt in order to determine the proportion of nonovigerous females that would extrude eggs during the current season.

The proportion mature by 3-mm size intervals was calculated and modeled with the logistic equation $Y = a/(1 + e^{b+cX})$ using the SAS Non-Linear Regression Procedure (SAS Inst. 1985).

The maturity curves (Fig. 10) indicate considerable variation in size-at-maturity. In Buzzards Bay, the estimate of L_{50} (carapace length at 50% maturity) was 76 mm, while 79% were estimated to be mature at minimum legal size (81 mm when study was conducted). Results from the two southern Gulf of Maine regions, Cape Cod Bay and Boston Harbor, were similar to one another. Their L_{50} estimates were 87 mm, while their proportions mature at minimum size were 18 and 27%, respectively. Size-at-maturity was slightly higher in the more northern Gulf of Maine region of Cape Ann, where the L_{50} was 90 mm, and the proportion mature at minimum legal size was estimated at 20%. The largest size-at-maturity was found in the outer Cape Cod region, where the L_{50} was 97 mm and only 12% were mature at minimum legal size. Predicted proportions mature at a proposed minimum size of 84 mm CL were ~33% for inshore Gulf of Maine regions, 17% off outer Cape Cod, and 89% in Buzzards Bay.

Size-at-maturity is related to summer water temperature (Templeman 1936); high summer temperatures enhance maturation at small sizes. Lobster in Buzzards Bay are subject to the highest maximum summer water temperature of any region sampled. Buzzards Bay is a shallow embayment with an average depth of only 11 m (Anraku 1964) and maximum bottom temperatures of about 21°C (Colton and Stoddard 1973). Shallow waters prevent the development of a thermocline; Anraku (1964) and Rosenfeld et al. (1984) noted summer vertical temperature gradients of less than 3°C.

Conditions are quite different in relatively deeper areas of the Gulf of Maine and east of Cape Cod, where substantial thermoclines exist during summer and bottom temperatures are inversely proportional to depth. Bigelow (1927) reported that Cape Cod Bay temperatures were higher than the other Gulf of Maine regions due to the shoal water and partial enclosure created by the peninsula of Cape Cod. Boston Harbor waters, which are relatively shallow and sheltered by several islands, experience similar warming. The common L_{50} values of these two regions reflect their comparable temperature regimes.

Finally, the waters off Cape Ann and east of Cape Cod are considerably deeper and colder than other inshore regions. This is reflected by the elevated sizes-at-maturity observed there. Furthermore, the historical occurrence in these regions of tagged lobster from Maine and Canadian studies and V-notched females, presumably from Maine, suggest that migrant lobster are more abundant here than in other regions sampled.

Despite a few exceptions, the annual proportions of females ovigerous during the 1981-86 study period were very similar within each region (Table 19). Lower-than-normal sampling intensity during the height of egger availability off outer Cape Cod in 1981 and in Buzzards Bay in 1981-82 may have caused the indices for those years to be below the 6-year average. However, the four Gulf of Maine regional indices were consistently at or below 5%, with Cape Ann averaging higher than the others. Six-year means for outer Cape Cod and Buzzards Bay were 24%.

The 6-year mean carapace lengths of "eggers" in the Beverly-Salem, Boston Harbor, and Cape Cod Bay regions were similar (84.0, 82.5, and 85.4 mm, respectively) compared with the relatively large means of 97.2 and 107.5 mm for Cape Ann and outer Cape Cod, respectively (Table 20). Buzzards Bay females averaged lowest at 80.3 mm.

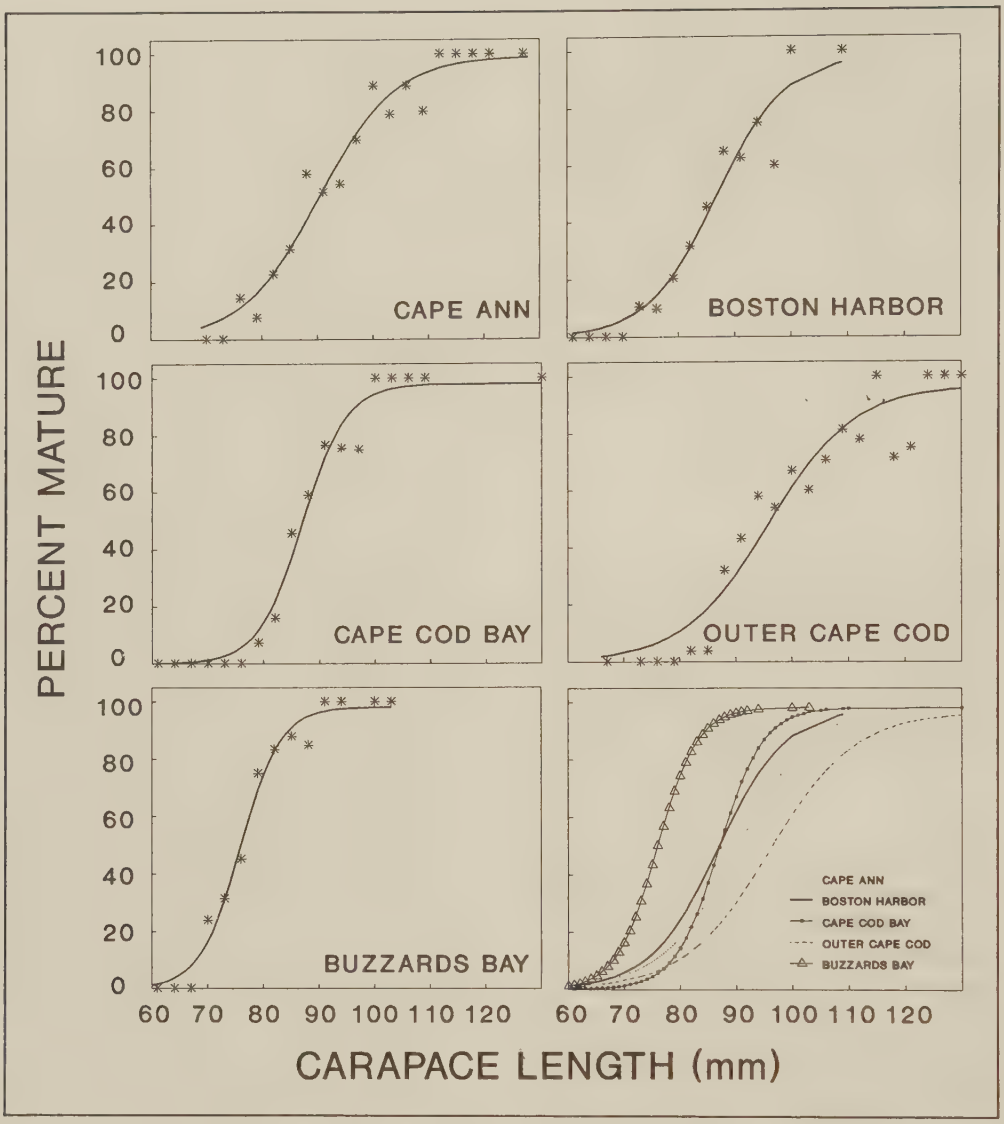

Figure 10

Functional size-maturity relationships for female American lobster from five coastal Massachusetts regions, 1986 (*observed data in 3-mm groupings).

Table 19

Percent of females ovigerous, statewide and by region, for all American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986	Mean
State	5.9	7.7	10.9	9.1	8.6	9.1	8.6
Cape Ann	1.7	3.1	4.4	3.2	4.6	5.0	3.7
Beverly-Salem	1.7	2.8	1.2	0.4	1.9	1.1	1.5
Boston Harbor	—	—	—	1.4	1.2	2.0	1.5
Cape Cod Bay	3.9	3.1	3.7	3.1	3.2	2.1	3.2
Outer Cape Cod	11.1	23.0	30.3	26.8	22.3	28.9	23.7
Buzzards Bay	16.0	16.9	32.5	26.6	25.0	25.3	23.7

Table 20

Mean carapace length (mm) of all ovigerous female American lobster, statewide and by region, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	88.5	87.6	88.6	87.4	87.9	88.1
Cape Ann	109.0	100.3	94.3	90.5	93.8	95.0
Beverly-Salem	80.5	84.5	85.8	83.5	85.9	83.5
Boston Harbor	—	—	—	82.1	84.0	81.3
Cape Cod Bay	86.4	83.8	85.5	84.4	85.2	86.8
Outer Cape Cod	109.8	106.1	108.0	107.1	106.9	107.3
Buzzards Bay	78.1	79.6	81.6	83.0	80.1	79.4

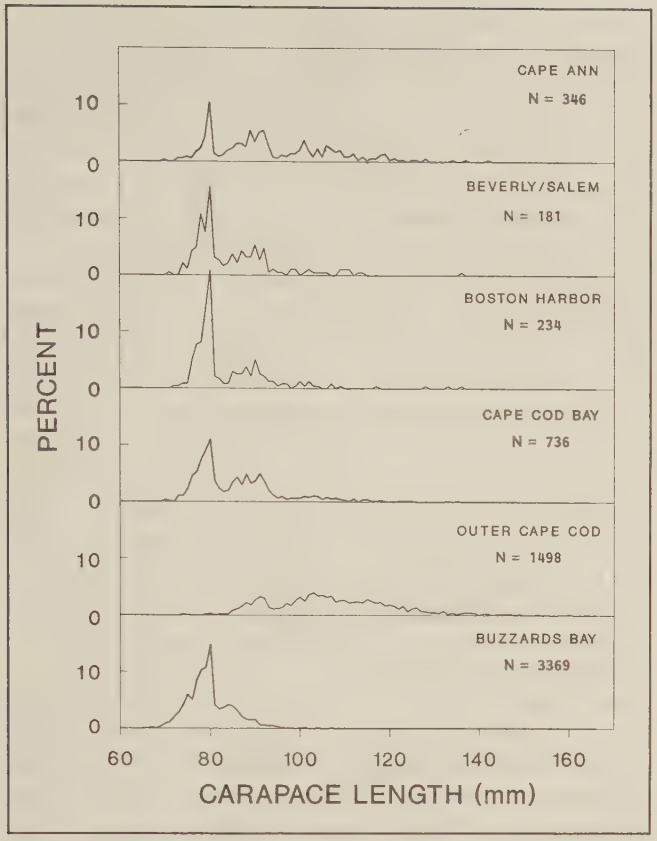

Figure 11
Comparison of 1981-86 summaries of ovigerous female American lobster size-frequency data from six coastal Massachusetts regions.

The abundance and size of ovigerous females are functions of the size-at-maturity and fishing pressure. Regardless of maturity status, most legal-sized females (over 95% in inshore Gulf of Maine regions) reach the market before extruding eggs. The highest fishing-pressure index was found in Buzzards Bay where only a relatively small percentage of eggers were legal-sized (6-year mean 34.4%; Fig. 11). Sublegal eggers were abundant there because most females mature before minimum legal size. Briggs and Mushacke (1979) computed a similar average berried-female length of 80 mm (range 64-120 mm) in western Long Island Sound.

The southern Gulf of Maine regions also exhibit high fishing-pressure indices (89-95%); however, few lobster are mature at minimum legal size due to elevated sizes at 50% maturity (87-90 mm). Eggers are far less numerous there than in Buzzards Bay and tend to be of larger size (except for the Boston Harbor region, Fig. 11). Six-year mean percentages of all egg-bearing females larger than minimum legal size were: Cape Ann 79.6%, Beverly-Salem 55.5%, Boston Harbor 35.3%, and Cape Cod Bay 54.5%.

Outer Cape Cod exhibited a high frequency of large egg-bearing females (99.5% were legal-sized). The largest size at 50% maturity (97 mm) was observed in this region. A very low fishing-pressure index (6-year mean 44%) contributes to the survival of the numerous large-sized eggers there (Fig. 11).

Table 21
Cull rate (%), statewide and by region, for all American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	10.0	10.8	10.7	14.8	18.1	20.9
Cape Ann	10.0	9.8	10.5	11.5	23.9	25.3
Beverly-Salem	8.3	8.6	10.2	20.9	23.0	30.0
Boston Harbor	—	—	—	13.3	19.3	19.1
Cape Cod Bay	11.1	10.7	10.9	15.6	18.3	21.6
Outer Cape Cod	5.7	11.3	8.9	13.0	13.4	16.1
Buzzards Bay	13.5	14.7	12.4	12.4	13.4	14.6

Both Cape Ann and Outer Cape Cod regions exhibited a higher proportion of eggers ≥100 mm CL than other inshore regions. This is consistent with our V-notched female size-frequency observations. Sixty-six percent of the V-notched lobster observed off Cape Ann and 80% of those observed off outer Cape Cod were larger than 100 mm CL. The influx of large offshore lobster, as well as migrants from the northern Gulf of Maine areas off Maine and Canada, apparently contribute to these wider size distributions.

Similar observations were reported by Briggs and Mushacke (1980) on the south shore of Long Island, New York. They noted an average berried-female carapace length of 99 mm (range 78-135 mm) and found only nine sublegal eggers. Size distribution in this area was thought to reflect mixing of large offshore migrants. This relatively open area with a greater depth range is comparable to outer Cape Cod and Cape Ann regions which exhibited similar large average lengths of egg-bearing females with few ovigerous females less than minimum length.

Culls

The percentage of culls (lobster with missing or regenerating claws) among all lobster sampled in Massachusetts coastal waters ranged from 10.0% in 1981 to 20.9% in 1986 (Table 21). Coastwide indices for 1981-83 were statistically equal, but those for 1984, 1985, and 1986 were significantly greater and different from one another (Duncan's Multiple Range Test, $P = 0.05$). Legal, marketable, and sublegal size categories exhibited similar trends (Tables 22-24). Indices were generally higher for sublegals than for legals, a bias which is assumed related to multiple recaptures (and handling) of sublegals. Similar sublegal trends have been reported by Briggs and Mushacke (1979, 1980).

The 6-year trend depicted an escalated number of culls in all regions except Buzzards Bay where the incidence remained relatively stable. Until 1984, Buzzards Bay exhibited the highest cull rate which was possibly related to its high fishing-pressure index (highest among coastal Massachusetts regions) and consequently high "throw back" rate. However, during 1984 most regional cull rates increased substantially while the Buzzards Bay rate remained unchanged.

Table 22

Cull rate (%), statewide and by region, for American lobster ≥81 mm carapace length, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	8.1	9.7	9.2	12.7	14.8	17.0
Cape Ann	10.7	9.6	7.5	10.4	19.4	20.3
Beverly-Salem	4.3	7.7	7.4	15.5	19.3	22.1
Boston Harbor	—	—	—	10.1	16.2	15.8
Cape Cod Bay	9.3	9.3	10.0	13.2	14.5	18.1
Outer Cape Cod	5.3	10.3	8.1	13.3	12.5	14.9
Buzzards Bay	16.1	13.2	12.7	12.3	13.8	13.6

Table 23

Cull rate (%), statewide and by region, for marketable American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	8.2	9.9	9.2	13.2	16.2	17.6
Cape Ann	10.8	9.8	7.3	10.5	20.9	20.7
Beverly-Salem	4.4	8.0	7.4	15.6	18.5	22.2
Boston Harbor	—	—	—	10.2	16.2	15.7
Cape Cod Bay	9.3	9.3	10.0	13.2	15.9	18.2
Outer Cape Cod	5.3	10.9	8.6	14.8	12.9	16.8
Buzzards Bay	16.9	13.1	12.3	12.6	15.4	14.1

Table 24

Cull rate (%), statewide and by region, for American lobster <81 mm carapace length, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	11.2	11.5	11.6	16.1	20.2	23.2
Cape Ann	8.0	10.6	12.6	12.2	26.9	28.7
Beverly-Salem	10.0	9.0	11.2	22.3	24.0	31.8
Boston Harbor	—	—	—	14.5	20.5	20.0
Cape Cod Bay	11.9	11.3	11.4	17.0	20.2	23.4
Outer Cape Cod	7.8	17.9	13.5	11.7	18.6	22.8
Buzzards Bay	12.7	15.2	12.2	12.4	13.3	14.9

This escalating cull rate may have reflected increased fishing effort throughout coastal waters by mobile and fixed-gear fishermen (Buzzards Bay is closed to trawling). Commercial traps fished increased by 34% during the study period, which certainly enhanced the handling of lobster. Also, this increased effort entrapped more lobster with other aggressive predators (lobster and finfish). These aggressive encounters may be enhanced in wire traps which appear to reduce escapement of sublegal lobster. In addition, these traps have a reputation for causing culls because lobster are more difficult to remove when they grasp the wire strands; however, culling may vary with the individual lobsterman depending upon his level of patience and care. The increased use of traps (wood or wire) is a plausible explanation for much of the increased cull rate, especially in nearshore waters where other fishing activities such as trawling or gillnetting are limited. Krouse (1976) noted a positive correlation between fishing intensity (trap density) and cull rate off the coast of Maine.

We have detected extraordinarily high cull rates during certain months in the Cape Ann region, which may be caused by fishing activities other than pot fishing. The traps sampled in this region were moved east to deeper water (≥120-ft contour) in the autumn. Cull rates of 49% and 53% were subsequently observed during October and November, respectively, in contrast to rates of 9-25% during May-September in shoaler waters. The higher incidence appears to be a function of the area fished rather than seasonality. This deepwater area is open to trawling by special permit only during 1 Feb-31 March and 15 June-30 Sept, while the shallower area is closed to trawling all year.

Russell et al. (1978) found a higher incidence of culls on mud bottom near a trawlable area of Rhode Island Sound than on ledges elsewhere (12.4% vs. 10.3%). They inferred that trawl-induced damage was the cause. Other studies documented enhanced shell damage and cull rate from bottom-trawl activity particularly during the molt period (Currier 1984, Estrella 1989, Ganz 1980, Smith and Howell 1987). Also, the effect of gillnetting on lobster cull rates needs investigation.

It is also possible that lobster which are behaviorally subordinate due to culling are forced to congregate on less than optimal habitat, i.e., relatively flat, open areas of sand or mud which lack structure. However, this hypothesis has yet to be proven.

Claw loss may also occur naturally as a result of environmental or molting conditions. Adverse weather, which results in strong winds and heavy seas that jostle or damage traps, may cause culls. Briggs and Mushacke (1980) documented the effects of a hurricane in greatly increasing the cull rate. This problem may be particularly acute if trap movement occurs while claws extend through mesh or lathe spacing. Autotomy (reflex amputation of an appendage) may be induced by damage or overstimulation of the limb nerve (Cobb and Phillips 1980). A molting lobster which encounters difficulty in withdrawing a claw through the narrow segment at the base of the old claw will drop this claw in order to complete the molt. The proportion of culls occurring in this manner is unknown.

Trap mortality

The incidence of dead lobster in traps coastwide was always less than 1 percent annually (0.04-0.22%; Table 25) during the 6-year study period. Indices for legal and sublegal size groups were also less than 1 percent (Tables 26-27). This parameter value may vary seasonally and can be enhanced by environmental stresses, molting, intra- and interspecific

Table 25

Percent trap mortality, statewide and by region, for all American lobster sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	0.15	0.04	0.22	0.15	0.18	0.20
Cape Ann	0.00	0.00	0.00	0.27	0.03	0.16
Beverly-Salem	0.00	0.00	0.00	0.00	0.04	0.22
Boston Harbor	—	—	—	0.00	0.03	0.03
Cape Cod Bay	0.00	0.02	0.03	0.00	0.00	0.02
Outer Cape Cod	0.46	0.22	0.23	0.48	0.40	0.85
Buzzards Bay	0.62	0.00	1.13	0.43	0.76	0.25

Table 26

Percent trap mortality, statewide and by region, for American lobster ≥81 mm carapace length, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	0.16	0.04	0.26	0.20	0.23	0.29
Cape Ann	0.00	0.00	0.00	0.10	0.03	0.22
Beverly-Salem	0.00	0.00	0.00	0.00	0.00	0.49
Boston Harbor	—	—	—	0.00	0.04	0.04
Cape Cod Bay	0.00	0.00	0.00	0.00	0.00	0.00
Outer Cape Cod	0.39	0.16	0.18	0.51	0.36	0.71
Buzzards Bay	0.62	0.00	1.46	0.40	0.96	0.28

Table 27

Percent trap mortality, statewide and by region, for American lobster <81 mm carapace length, sampled during commercial lobster trap-catch survey, Massachusetts coastal waters, 1981-86.

	1981	1982	1983	1984	1985	1986
State	0.15	0.03	0.20	0.12	0.15	0.15
Cape Ann	0.00	0.00	0.14	0.39	0.02	0.12
Beverly-Salem	0.00	0.00	0.00	0.00	0.05	0.16
Boston Harbor	—	—	—	0.00	0.02	0.02
Cape Cod Bay	0.00	0.03	0.05	0.00	0.00	0.03
Outer Cape Cod	0.87	0.65	0.50	0.31	0.62	1.62
Buzzards Bay	0.62	0.00	0.94	0.45	0.68	0.24

aggression during entrapment, pollution, or the synergistic effect of these factors.

Lobster mortality in the wild may be attributed to a number of causes (Sindermann 1979). Gaffkemia, a naturally occurring disease of the blood, has received the greatest notoriety as a potential lobster killer. It has claimed many crustaceans in lobster impoundments; however, no one has been able to assess its contribution to natural mortality. Young (1973) related documented lobster mortality off the New Jersey coast to a possible synergistic effect of low dissolved oxygen, high temperatures, and gill fouling due to copious suspended flocculated material. McLeese and Wilder (1964) found death ensued when the chitinous covering of the gills was attacked by shell disease, subsequently interfering with respiration.

High temperature, low dissolved oxygen and salinity, pollution, predation, and intra- and interspecific aggression during entrapment may be particularly detrimental during stressful periods such as ecdysis. It is at this time that lobster are most vulnerable, particularly to physical damage. The crowded conditions that potentially can occur in a lobster trap enhance aggressive behavior which is less frequently displayed in the wild (Atema and Cobb 1980). Such behavior may be particularly lethal to relatively defenseless, recently molted, lobster. Nevertheless, the 6-year record indicates that trap mortality is consistently low and does not represent a problem to this fishery.

Summary

The Massachusetts coastal lobster (*Homarus americanus*) resource was profiled and its condition assessed with CPUE and biological data collected at sea and at dealerships. The use of a commercial lobster sea-sampling program to provide valid assessment statistics was described. Between 1981 and 1986, six coastal regions were sampled monthly, with an areal and temporal data weighting design.

An improved index of catch per trap haul/set-over-day was generated by modeling the relationship between catch and immersion time and standardizing effort to our survey modal value of 3 set-over-days. The coastwide annual mean catch rate ranged from 0.696 to 0.825 marketable lobster per trap during the study period. No significant difference was found among 1981-83 indices, but a significant decline occurred in 1984 followed by a significant increase to the 1985-86 record levels. This 6-year time-series of mean annual catch rates tracked closely the landings trend for territorial waters.

Analysis of historical landings and effort trends between 1888 and 1986 indicated that substantial increases in both have occurred in recent years. However, CPUE increases may be due to changes in climate, larval survival, fishing habits and efficiency.

Six-year trends in biological parameters included a gradual increase in rates of exploitation and total annual mortality corresponding to a gradual decline in mean carapace length of marketable lobster. The frequency of culls among all lobster sampled ranged from 10.0% in 1981 to 20.9% in 1986. Escalation of cull frequencies occurred in all regions except Buzzards Bay where they remained relatively stable at about 14%. Causative factors are discussed, such as fishing effort, predatory activity, and ecdysis. The percentage of lobster found dead in traps was consistently less than 1%.

The sex ratio (%F:%M) differed significantly from 50:50 and approximated a 60:40 relationship during the study period. The effect on sex ratios of differential escapement by sexes through trap vents was investigated. A significant difference was found between the carapace length-width rela-

tionships of male and female lobster. Females exhibited significantly wider carapace widths than males in all regions sampled. Other factors affecting sex ratios were discussed. These include possible behavioral differences of sexes relative to maturation which may cause sex ratios to vary by depth. Also, ratios in favor of females may be a function of reduced growth rate of females in sublegal lobster and protection of egg-bearing females in legal-sized lobster.

A significant difference was found between the weight-length relationships of male and female lobster. This difference was evident in all six regions and was characterized by females weighing more than males at smaller sizes and less than males at larger sizes. A north-south clinal trend was evident, wherein lobster north of Cape Cod weighed less at length than those from regions south of Cape Cod.

A cement-gland staging technique was used to establish functional size-maturity relationships for female lobster in five coastal Massachusetts regions. Proportions mature at size represent more realistic values than those obtained by analyses of percent of females ovigerous, because the effect of fishing pressure in lowering the proportion ovigerous is circumvented.

Three lobster groups, differing in major population descriptors, are defined by our data. Lobster from the outer Cape Cod region exhibited the largest 6-year average carapace length of marketable lobster (96 mm), the lowest fishing-pressure index (44%), lowest total annual mortality ($A = 36\%$), and the largest size at which 50% of the females were mature (97 mm). The 1981-86 mean annual percent of females observed with eggs was 24%.

Buzzards Bay lobster exhibited the smallest 6-year average size of marketable lobster (85 mm), the highest fishing-pressure index (96%), the highest total annual mortality ($A = 98\%$), and smallest size at 50% maturity (76 mm). The 6-year mean percentage of females with eggs was also 24%.

Southern Gulf of Maine regions (Cape Ann, Beverly-Salem, Boston Harbor, and Cape Cod Bay) were intermediate in mean carapace length (87 mm), fishing-pressure index (92%), total annual mortality ($A = 92\%$), and size at 50% maturity (87-90 mm). The percentage of females with eggs was $\leq 5\%$.

Large migrant lobster (>100 mm CL, many of which were ovigerous females) from either offshore or Canadian and Maine waters were more numerous off Cape Ann and outer Cape Cod than in other Massachusetts coastal regions sampled. Geography may be a factor in concentrating these lobster, since these two regions are adjacent to steeply sloping gradients which lead to a much greater depth range than is available to other coastal regions sampled.

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